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UNUSUAL TIMING OF COPULATIONS IN THE AUSTRALIAN BRUSH-TURKEY

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ABSTRACT.—Recent studies of sperm competition have shown that the timing of copulations can be crucial to fertilization success. For example, in some birds copulations that occur near the time of laying are less likely to fertilize eggs than copulations that occur at other times. Thus, it was surprising to find that in Australian Brush-turkeys (*Alectura lathami*), most within-pair copulations (61.2%) occurred less than 1 h before laying, typically providing only 25 to 40 min for sperm to reach storage organs before potentially being flushed out by the descending egg. Brush-turkeys incubate their eggs in large mounds constructed by males; females lay an egg every few days and bury it within a chosen mound. Females usually solicited a copulation within 2 to 3 min after arriving at a mound to lay, but some males still forced copulations, particularly during the latter portion of laying visits. The unusual prevalence of copulations before laying probably results from males having little information about or control over female copulation behavior except when females need to lay in a males' mound. The prevalence of forced copulations during the latter part of laying visits may indicate conflict between the sexes over what constitutes adequate "payment" by females for use of a male's incubation mound. Neither sex showed any interest in copulating immediately after an egg was laid. This observation does not support the idea of a "fertilization window" after laying, but instead indicates that copulations at this time are probably ineffective in fertilizing eggs. Females also frequently made nonlaying visits to incubation mounds. The 38.8% of within-pair copulations that occurred during nonlaying visits may have been more likely to fertilize eggs, but the timing of these visits was controlled by females, who were probably less likely to be subject to male control when not laying. *Received 14 July 1997, accepted 18 June 1998.*

MALES AND FEMALES may have different agendas regarding the timing and frequency of copulation, and conflicts may arise over when copulations should occur and with whom (Davies 1992, Birkhead and Møller 1993, Westneat 1996). As a result, males and females may try to manipulate the copulation behavior of one another. To do so, both sexes have evolved strategies that are influenced by their reproductive roles and physiologies. Males may mate with females frequently to swamp other males' sperm, or they may force females to copulate (Birkhead and Møller 1992). Females may resort to more subtle tactics, including extrapair copulations that are timed to minimize or maximize their effectiveness (Westneat et al. 1990, Westneat 1996).

In birds, ova typically are fertilized within 2 h of ovulation, and the timing of a male's copulations relative to ovulation can be crucial to his fertilization success for at least two reasons. First, although sperm can be stored in tubules in the reproductive tracts of females for several weeks (Birkhead and Møller 1992, Briskie and Montgomerie 1993), it is lost passively over time, giving males that copulate close to the time of ovulation an advantage in fertilization (Birkhead et al. 1995, Colgrave et al. 1995). Second, although ovulation follows egg laying, the presence of an oviducal egg may impede the uptake and storage of sperm, resulting in reduced fertilization success for copulations that occur too near the time of laying (Brillard et al. 1987, Birkhead and Møller 1992, Birkhead et al. 1995). Cheng et al. (1983) proposed that a particularly favorable time for insemination, the "insemination window," occurs after an egg is laid but before ovulation. However, evidence suggests that the period of reduced fertility observed before laying also lasts at least an hour after laying (Birkhead et al. 1995).

Birkhead et al. (1995) argued that the timing of inseminations relative to egg laying in most

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bird species might not be especially important in determining the outcome of sperm competition, because the majority of species copulate only infrequently once egg laying has started. However, the Australian Brush-turkey (*Alectura lathami*) copulates regularly throughout a several-month breeding season, and females often copulate immediately before laying.

Australian Brush-turkeys (family Megapodiidae) are endemic to forests of eastern Australia (Jones and Birks 1992, Jones et al. 1995). Male Brush-turkeys provide all postlaying parental care to chicks by building and maintaining large incubation mounds constructed of soil and vegetation (Jones 1988). Males may build more than one mound each year and/or usurp mounds of competitors (Jones 1990a, Birks 1996); they also spend several hours per day tending mounds by mixing in fresh leaf litter and aerating them. Incubation heat is produced from microbial decomposition within mounds (Seymour and Bradford 1992), which can accommodate the eggs of several females at one time. After the eggs hatch, the super-precocial chicks dig their way out of the mound and are completely independent from further parental care.

Brush-turkey females typically lay one egg every few days in a hole they dig within a chosen incubation mound. They do not lay "clutches" in a traditional sense but instead usually lay a series of about 5 to 10 eggs with one male over a period of three to four weeks, then switch to a new male and lay another series of eggs, laying in up to five different mounds per season (Birks 1996). Some females lay more than 20 eggs per year (Birks 1996).

Brush-turkeys have no social pair bonds. Females visit and copulate with multiple males each year, and 20 to 45% of eggs in a male's mound may be sired by rival males (Birks 1997). Because females do not usually associate with males except at incubation mounds (Jones 1990b), males have no control over female behavior away from mounds and have little information about whether females are copulating with other males. In addition, whereas females may visit males at any time, the only time a male is guaranteed a visit is when a female is about to lay an egg. Given the evidence that inseminations occurring at this time are less likely to fertilize eggs, this aspect of female behavior may make it difficult for males to control fertilizations.

Brush-turkeys are excellent subjects for studying sexual behavior because their unusual ecology and mating system have direct consequences for the timing of copulations, and they thus provide insight into how these forces may shape copulation behavior in other birds. In addition, copulations are obvious and take place at predictable locations and times; i.e. on top of incubation mounds when females visit these mounds during the morning hours.

Here, I present results of a study of Australian Brush-turkeys in which I: (1) describe copulation behavior, with information on the timing, frequency, and type of copulations; and (2) discuss possible reasons for the unusual timing of solicited and forced copulations within the context of potentially conflicting male and female interests.

STUDY AREA AND METHODS

I collected the data presented here during a four-year study of Australian Brush-turkeys in North Tamborine Environmental Park, a small subtropical rainforest reserve in southeastern Queensland (see Jones 1987). Birds were caught in drop-traps and marked with numbered steel leg bands and colored patagial wing tags. I collected behavioral data from July to December, 1989 to 1992, but because many individuals were unmarked in 1989, I used only data from marked individuals observed from 1990 to 1992 for analyses here. Six to eight males and 11 to 13 females bred in the approximately 8-ha park each year; most (ca. 80%) of the breeding males and females were present during at least two of the three years.

There were 9 to 14 ($\bar{x}$ = 11.0 ± SD of 2.16) active brush-turkey mounds in the study area each year. Mounds were individually numbered and mapped, and inactive mounds were monitored for new activity weekly. Behavioral observations were made from hides and in 1991 and 1992 with three or four Sony CDF-55 8-mm video cameras placed on tripods at active incubation mounds. Previous studies at this site have shown that copulations are confined to incubation mounds (Jones 1990b). Most behavioral observations were made in the morning (dawn to ca. 0900) because the vast majority (>90%) of mating activity takes place at this time (Jones 1987). All active mounds within the park were observed regularly. By watching three to six mounds simultaneously, most mounds could be observed for three to five days each week. Behavioral observations at mounds totaled 898 watches and 2,316 h, and mounds that persisted and received eggs were watched an average of 54.3 ± 15.4% of the days that they were active (n = 28

mounds). Detailed information was collected on all behaviors, including copulation, laying, and inter- and intrasexual aggression (Birks 1996).

Behavior was also noted at other sites and times of day, including 200 h of afternoon mound measurements, 260 h of trapping and observing birds at feeding sites baited with grain, and 10 h of observations at roost sites in the evening. Two mounds within sight of my residence were monitored casually for activity throughout the day.

I referred to visits where an egg was laid as "laying visits" and other visits as "nonlaying visits" (Birks 1996). Laying visits were less common than nonlaying visits, comprising only 30.0% of all visits to mounds (213 of 711 observed visits). However, laying visits usually were longer than nonlaying visits (49.4 ± 22.2 min vs. 20.6 ± 24.8 min), and female behavior differed between the two types of visits. During typical laying visits, females spent about 30 min digging an egg-laying hole, whereas during nonlaying visits they spent more time watching mounds and less time digging (Birks 1996).

For these analyses, visits were included only if all copulations were observed. Where possible, I controlled for individual differences by summing copulation behavior by female; where sample sizes for particular behaviors (e.g. forced copulations) were too small to do this, I gave the number of individuals observed. I categorized female copulations as within pair or extrapair (EPC) based on a previous finding that females usually laid in one incubation mound for several weeks, during which time they copulated almost exclusively with the male tending that mound (i.e. the "pair" male; Birks 1996, 1997). Copulations usually lasted 2 to 3 s. Three distinct types of copulations occurred: solicited copulations, unsolicited copulations, and forced copulations (for a detailed description see Birks 1996; also see Westneat et al. 1990). Solicitations nearly always resulted in behaviorally successful copulations. Unsolicited copulations, which also were usually successful, were initiated by males but passively accepted by females. Forced copulations were also initiated by males, who mounted a female while she attempted to avoid him. A male could sometimes subdue an uncooperative female by pulling on her neck with his beak while simultaneously pushing her body down with his wings. No discernible differences occurred in female behavior following a forced copulation versus one that was solicited or unsolicited; females generally remained on the mound after copulating.

Results

General copulation behavior.—Females copulated only with males who had active incubation mounds (i.e. mounds that were tended daily by the male and that had reached or nearly reached a stable incubation temperature). Dow (1988) reported that some copulations occurred more than 100m from incubation mounds in a population in open, dry forest. In my study area, however, copulations appeared to be confined to incubation mounds or to the area immediately surrounding the base of mounds (see also Jones 1990b).

Females copulated with an average of 2.4 ± 1.0 males per breeding season (n = 15 females for 29 female breeding seasons). Once females began laying for the year, they laid an egg about once every two to five days (see Birks 1996). Females copulated during nearly every laying visit, sometimes returning to solicit copulations with the same male between laying visits (see below). Females copulated on average 3.0 ± 1.1 times per egg and laid an estimated average of 12.6 ± 9.0 eggs per season at the study site (they may have laid more eggs at nearby sites). Males usually copulated one to three times on mornings when one or more females visited, with a maximum of seven copulations observed in one morning. However, even the most "popular" males frequently had mornings with no copulations. Males averaged 1.2 ± 0.4 copulations per day during the period when their mound was active, and 62.4 ± 35.6 copulations per breeding season (n = 9 males for 19 male breeding seasons).

Only 30 extrapair copulations were observed (4.5% of copulations). All EPCs except one occurred on days when the female involved did not lay. EPCs occurred throughout the breeding season and, by definition, only during nonlaying visits. However, no discernible pattern or predictor of EPCs existed; they seemed to be byproducts of females attempting to avoid male harassment during mound sampling (Birks 1996).

Timing of copulations.—Most within-pair copulations (61.2%) took place during laying visits; the remainder occurred during nonlaying visits. Females frequently copulated multiple times (up to seven) during laying visits, whereas they usually did not copulate, or copulated only once, during nonlaying visits (Fig. 1). Differences in the average number of times females copulated during laying visits (1.8 ± 0.37) and during nonlaying visits (0.6 ± 0.22) were significant (paired t-test assuming unequal variances, $P < 0.001$).

Females copulated on 91.5% of laying visits.

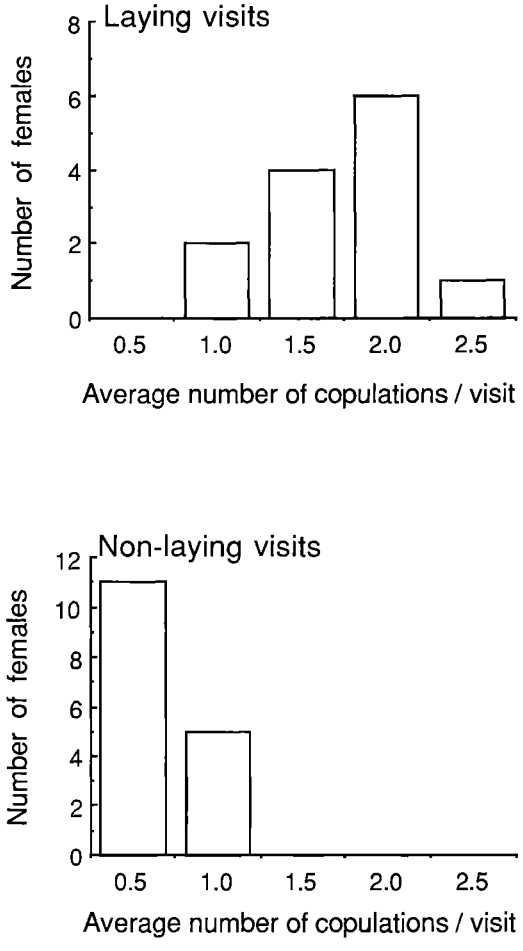

FIG. 1. The average number of copulations that occurred for each female during laying visits (top) and nonlaying visits (bottom). Means were included only for females with at least five visits of that type; female sample size is slightly higher for nonlaying visits (n = 16 females for 303 copulations) than laying visits (n = 13 females for 341 copulations) because three females had at least five nonlaying visits but fewer laying visits.

During most of the 18 laying visits when females failed to copulate, something unusual happened during the visit to interfere with normal copulation behavior. For example, males were absent from their mounds during 3 of these 18 visits (males were absent occasionally when they tending more than one mound simultaneously). During most of the remaining 15 visits, females were subjected to unusual levels of intrasexual aggression and as a result dramatically shortened their laying behavior (Birks 1996). Although females did not copulate as frequently during nonlaying visits, these visits were more common, and copulations happened regularly between days of laying. Females were observed returning to the same male to solicit copulations between successive eggs 28.1% of the time (n = 16 females for 146 intervals between eggs).

If females copulated during a visit, their first copulation usually occurred immediately after they arrived at the incubation mound. During laying visits, the median time between a female's arrival at the mound and her first copulation was 2 min, and 83.7% of all copulations occurred within the first 10 min of the visit (n = 196 visits by 17 females). Similarly, during nonlaying visits in which females copulated (n = 210), the median time until first copulation was 3 min, with 82.8% of copulations occurring during the first 10 min of visits.

During laying visits, all copulations took place before the egg was laid. As a result, the time between copulation and laying was short (Fig. 2), with a mean of 37.1 min (range 8 to 94 min) between a female's first copulation and laying, and only 25.4 min (range 2 to 81 min) between her last copulation and laying (on visits where females copulated more than once). After laying, a female covered her egg briefly (ca. 1 to 5 min) and then left the mound; the male finished burying the egg. Neither sex showed any interest in copulating after laying.

Initiation and control of copulations.—Males attempted to control female copulation behavior through general aggression and forced copulation attempts. Males appeared to allow females access to their mounds on a quid pro quo basis; i.e. females were "expected" to solicit copulations regularly with the male if they were to continue visiting his mound. Males never completely denied females access to their mounds, but they sometimes chased females away from their mounds after only a brief visit. Females were chased away from mounds by males on 59 occasions (8.0% of visits). On all other visits, females left independently, or, less commonly, were chased away by another female (Birks 1996). However, the likelihood that a female would be chased away during a visit to a male's mound was strongly influenced by her history of copulations with him. In the 46 cases involving single females who were chased away from incubation mounds (vs.

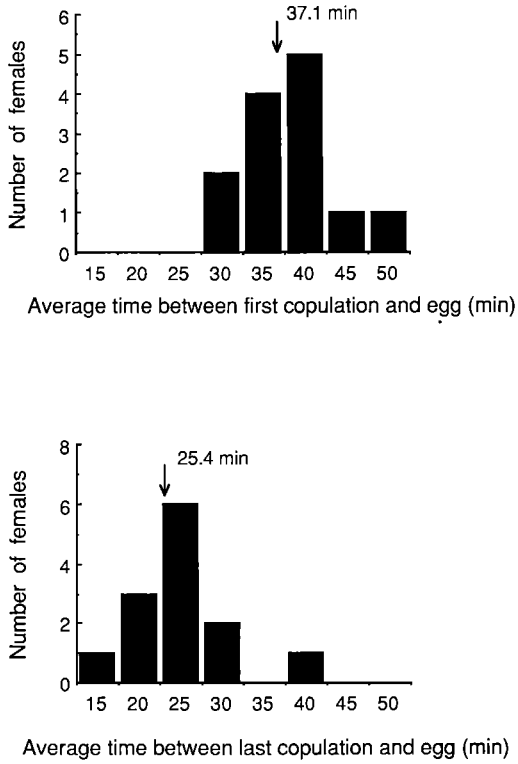

FIG. 2. The average length of time between a female's first copulation and laying during laying visits (top) and between her last copulation and laying for visits where females copulated more than once (bottom). Arrows indicate mean times; n = 13 females.

those in which several females were present), females that had not copulated with the male during a previous visit were more likely to be chased away than females that had copulated with him previously ($\chi^2 = 5.5$, df = 1, $P = 0.02$).

Most behaviorally successful copulations of known type were solicited by females (87.2% of 501). Unsolicited (6.6%) and forced (6.2%) copulations were less frequent. All nine breeding males attempted forced copulations regularly (20% of copulations) but usually were unsuccessful. Only 24.1% of forced copulation attempts (31 of 133) were successful, versus 96.5% of unsolicited and solicited copulations (470 of 487). Twelve of the 13 females who were observed laying at least five times experienced forced copulations or attempts, with an average total of 7.8 ± 6.6 such attempts per female during three breeding seasons.

Forced copulation attempts were much more common during laying visits than during nonlaying visits. Males attempted at least one forced copulation during 29.0% (62 out of 214) of laying visits, but only 9.8% (24 out of 246) of within-pair nonlaying visits had any forced attempts ($\chi^2 = 22.6$, df = 1, $P < 0.001$). Successful forced copulations occurred on 7.9% of laying visits (n =17) and 2.4% of within-pair nonlaying visits (n = 6).

Males did not appear to force copulations because females had not copulated with them previously or recently. During 78.0% of laying visits in which a forced copulation attempt occurred, the female had already solicited a successful copulation from the same male that morning. In addition, forced attempts were as frequent during visits by females who had copulated on more than one previous visit with the male (23.1% of 89 visits) than by females who had not (29.2% of 307 of visits; $\chi^2 = 1.15$, df = 1, $P = 0.28$), and were as frequent during visits made by females who had previously laid an egg in the male's mound (22.8% of 219 visits) as they were by females who had not (25.9% of 177 visits; $\chi^2 = 0.45$, df = 1, $P = 0.53$).

Timing of forced copulations.—During laying visits, the timing of forced copulation attempts relative to other copulations was not random. When series of copulations during single visits were analyzed according to type, forced copulation attempts occurred later in laying visits than expected by chance ($\chi^2 = 13.0$, df = 4, P = 0.01; Fig. 3). Only 22.0% of first copulations or attempted copulations were forced, whereas forced copulation attempts occurred almost three times as often later in visits (61.0%, 60.6%, and 71.4% of 2nd, 3rd, and 4th copulations were forced attempts, respectively). In contrast, during nonlaying visits forced copulation attempts occurred with approximately equal probability throughout the visit (46.4%, 65.0%, 58.3%, and 57.1% of 1st, 2nd, 3rd, and 4th copulations were forced attempts, respectively; $\chi^2 = 0.87$, df = 3, $P = 0.84$).

DISCUSSION

Timing of copulations.—The timing of copulations relative to laying is unusual in Australian Brush-turkeys. Most other bird species decrease their rate of copulation dramatically after laying begins and may even stop copulating before a female's fertile period has ended, al-

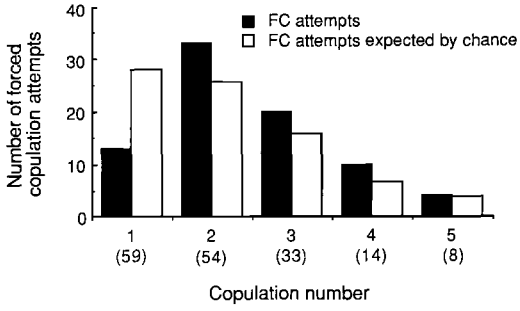

FIG. 3. Frequency of forced copulation attempts (both successful and unsuccessful) during the course of each laying visit in which they occurred. Shown are the actual number of forced copulation attempts that occurred during the 1st, 2nd, etc. copulation or attempted copulation, versus that expected by chance if forced copulation attempts were evenly distributed over time with respect to other types of copulations. Sample sizes (number of visits that had this many copulations) are indicated below copulation numbers.

though a minority (especially polyandrous species) continue copulating until the clutch is complete (Birkhead and Møller 1993). In addition, although most birds lay early in the morning, copulation immediately before laying is rare (Birkhead and Møller 1993). In contrast, brush-turkeys copulated and laid regularly throughout the breeding season and copulated most often immediately before laying. The former observation is consistent with studies that have shown that copulation occurs throughout the laying period in species where sperm competition is likely to be high. However, the latter pattern is unusual and may reflect efforts by males to take advantage of marginal copulation opportunities in a mating system where males have little control over female behavior but have high levels of parental investment.

Because more than 60% of within-pair copulations occurred during laying visits, the time between copulation and laying was usually less than an hour (sometimes only a few minutes), and sperm had little time to reach storage organs before being potentially flushed out by the descending egg. It is not known whether the 25 to 35 min that typically occurred between copulation and laying in this species are long enough for sperm to be stored. The high frequency of copulations directly before laying suggests that at least some of these copulations resulted in fertilized eggs. Sperm can reach ova or travel from the vagina to the infundibulum in less than 30 min in domestic fowl such as chickens and turkeys (McKinney et al. 1984), suggesting that this is enough time for sperm to move significant distances within the female reproductive tract for other galliforms, at least when no egg is present. However, copulations immediately prior to laying have been shown to have poor fertilization success in domestic fowl (Brillard et al. 1987, Birkhead et al. 1995). Thus, if sperm uptake and storage are similar in brush-turkeys, copulations that occurred during laying visits were probably less likely to fertilize eggs than copulations that occurred during nonlaying visits. Future studies of the physiological mechanisms of sperm competition in Australian Brush-turkeys could help determine whether any special adaptations for sperm uptake or storage exist that result from their unusual timing of copulations.

Females copulated regularly between laying visits, and because these copulations usually occurred at least a day after an egg was laid, they may have been more likely to fertilize eggs. This was also true for extrapair copulations, which, by definition, also occurred during nonlaying visits and thus were not subject to immediate interference from a descending egg. This may have given the few EPCs that did occur an advantage in fertilizing eggs. An analysis of paternity in brush-turkeys is consistent with this idea; a disproportionate number of offspring were apparently sired by EPCs (Birks 1997).

Of course, the pattern of copulations documented here begs the question as to why the majority of within-pair copulations occurred immediately prior to laying rather than at other times. Part of the explanation may be that intersexual conflict exists over the frequency of copulations, with males having more direct control of female behavior just prior to laying than at any other time. Females appear to have little flexibility in laying time, and they cannot afford to be interrupted frequently during digging if they are to dig an adequate hole (Birks 1996). As a result, females might be more likely to solicit copulations to avoid male harassment while digging, both to ensure that laying occurs in a suitable hole and to avoid the potential risk of injury from egg breakage. This is supported by the observation that females tended to solicit copulations immediately after

arriving at a mound, especially during laying visits.

It is obviously not in the interest of males to force copulations if they risk injuring potential mates or their eggs, or if they interfere too much with the laying process. However, the asynchronous nature of female laying may mean that males had less knowledge than usual of when females were fertile or were going to lay. In addition, the lack of pair bonds and the freedom of females to visit other males resulted in at least moderate levels of sperm competition (on average, 27.7% of eggs were sired by males other than the ones tending the mounds in which the eggs were laid; Birks 1997). Given these circumstances, males probably benefited by copulating whenever females visited, even if their behavior conflicted with female interests.

It is somewhat surprising that neither males nor females showed any interest in copulating immediately after laying. This may be partly because females had little incentive to stay after laying (males buried the eggs after they were laid), and thus males had less influence over them. However, this explanation seems weak given the total lack of interest shown by males, and it also cannot account for the lack of female interest in copulating before leaving the mound. A better explanation may be that copulations at this time are ineffective; the behavior is consistent with findings from studies of sperm competition in domestic fowl (Brillard et al. 1987, Birkhead et al. 1995). In contrast, the behavioral data from my study are in direct contradiction to what would be expected if a fertilization window existed after laying, when inseminations might be particularly successful (Cheng et al. 1983). If such a physiologically favorable opportunity existed, one would expect male and female brush-turkeys to at least occasionally show interest in copulating immediately after an egg was laid.

One problem with attempting to determine the effect of timing on the relative efficiency of copulations is that brush-turkeys ovulate irregularly, and little is known about their reproductive physiology. Most birds lay one egg every 24 h during the laying period, ovulation occurs about 23 h previous to an egg being laid, and the egg is usually fertilized within an hour after ovulation (Birkhead and Møller 1992, 1993). However, when the period between eggs is longer, the window of time during which the egg can be fertilized will depend on the timing of ovulation relative to laying. If ovulation occurs quickly after laying, then the next egg will probably be fertilized within a couple of hours and will spend several days in the oviduct (e.g. Sandhill Crane [*Grus canadensis*]; G. Gee *in* Birkhead and Møller 1992). However, if ovulation occurs 24 h prior to laying, an egg would spend less time in the oviduct, and fertilization would probably occur at least a day after the female had laid her previous egg (e.g. Ancient Murrelet [*Synthliboramphus antiquus*]; Astheimer 1985). If the latter scenario applied to brush-turkeys, then a female's next egg would not be fertilized until at least a day following a laying visit. Because laying visits are the only time a male has predictable access to females, this would make control of paternity difficult for males.

Male and female control of copulation behavior.—In most bird species, females control the timing and success of within-pair copulations (Birkhead and Møller 1992, 1993), presumably because they invest relatively more in their eggs than do males. However, in species with extensive male parental care, females may copulate more frequently than they require to ensure continued parental investment from one or more males (Davies 1992, Owens et al. 1995). In Australian Brush-turkeys, both sexes contribute enormously to the reproductive potential of the other. Although females do not provide parental care after laying, they do produce large, highly nutritious eggs, and they lay many more eggs than do females of most other bird species. Moreover, although males provide all postlaying care of eggs, they may accommodate many females without restricting their mating opportunities (Birks 1997). Thus, no clear *a priori* prediction exists as to which sex should control copulation behavior.

Males almost always attempted to entice females to visit their mound through courtship displays (Jones 1987). However, once females were on the mound, males occasionally chased them away after only a brief visit. The observation that females who had not previously copulated with males were most likely to be chased away indicates that males expected females to copulate in return for mound access. In addition, the prevalence of forced copulations late in laying visits suggests that conflict

existed about what constitutes sufficient "payment" for mound access, with females generally willing to solicit one or two initial copulations but sometimes reluctant to solicit more.

Males probably benefited more from multiple copulations than did females. Males responded immediately to female solicitations, initiated some copulation attempts, and regularly attempted to force copulations, whereas females only passively tolerated some copulations and actively tried to avoid others. Although females exerted some control by soliciting copulations and occasionally avoiding those that were unsolicited, males were able to control some copulations through physical force.

Many ornithologists have dismissed the idea that female birds copulate to avoid physical interference from males, but they have done so mainly because most females do not copulate immediately before laying, when a major danger of injury from male interference is the rupturing of a mature egg in the oviduct (Birkhead and Møller 1993). However, female brush-turkeys face a much higher risk of such injuries than other birds because most of their copulations occur less than an hour before laying, and their eggs are unusually large (10% of their body mass) and very thin-shelled for their size (an adaptation to facilitate gas exchange within the mound; Seymour et al. 1986, Booth 1988). Thus, the reproductive physiology of brush-turkeys and other megapodes may put females in a uniquely dangerous position in terms of tolerating male interference during laying. This potential danger, coupled with a female's need to cooperate with males in order to secure access to incubation mounds, may have led to the frequent solicitation of copulations during egg-laying visits, even if these copulations were less likely to fertilize eggs than those occurring during other visits to mounds.

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