The mating system of the White-throated Magpie-jay *Calocitta formosa* and Greenwood’s hypothesis for sex-biased dispersal

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Greenwood explained the different sex bias in dispersal of birds (usually female biased) and mammals (usually male biased) by a difference in mating systems: male birds primarily defend resources while male mammals primarily defend females. The White-throated Magpie-jay *Calocitta formosa* is unusual among birds in that females are philopatric and jointly defend permanent resource territories while males disperse before they are 2 years of age. One female in a group is the primary breeder. One male joins the group permanently as her mate. Males that do not have a permanent breeding position circulate among groups and attempt to mate with both the primary breeding female and other group females. Other females feed the primary breeder and her offspring and also pursue other reproductive behaviour, including secondary nesting in the territory and egg dumping into the primary breeder’s nest. I argue that the unusual dispersal pattern in this species is a result of the alternative reproductive strategies that can be pursued by males and females excluded from being primary breeders. The White-throated Magpie-jay conforms to Greenwood’s predictions: males pursue a mate defence rather than resource defence mating system and they are the dispersing sex. The primary factor influencing alternative reproductive tactics may be asynchronous reproduction among groups during the long breeding season arising from frequent renesting in an area of high nest predation.

One of the most striking differences between mammalian and avian social systems is the polarity of sex-biased natal dispersal (Greenwood 1980). With few exceptions, male mammals disperse farther than females (Clutton-Brock 1989), while, with even fewer exceptions, female birds disperse farther than males (Greenwood & Harvey 1982, Zack 1990). Greenwood (1980) explained this pattern by reference to differences in the common mating systems of birds and mammals: male birds primarily defend resources that females require, while male mammals directly defend females. In Greenwood’s view, the direction of a sex bias in dispersal is the result of the tactics that are pursued by the sexes to attain a breeding opportunity in a particular mating system. Where males defend territories, as in most birds, they typically remain near their natal territory because it provides an advantage in attaining their own territory (Arcese 1989, Zack 1990, Zack & Stutchbury 1992). Females disperse and search for a high-quality territory or mate (Bensch & Hasselquist 1992). On the other hand, when males defend females, young males disperse and search for mating opportunities, while females are philopatric, especially if dispersal costs are high (Clutton-Brock 1989). Although Greenwood favoured inbreeding avoidance as a general explanation for sex-biased dispersal, this causal factor remains controversial (Moore & Ali 1984, Dobson & Jones 1985, Waser 1985, Pusey 1987, Johnson & Gaines 1990). Nevertheless, Greenwood’s hypothesis for the direction of the sex bias remains valid even if other mechanisms besides inbreeding avoidance cause dispersal in the first place (Moore & Ali 1984). As Greenwood (1980) noted in his paper, what is lacking to verify or disprove his contention are detailed studies of mammals or birds which show a reversed pattern of sex-biased dispersal (see also Arcese 1989, Johnson & Gaines 1990).

White-throated Magpie-jays *Calocitta formosa* are cooperative breeders which defend large, permanent resource territories (Skutch 1953, T.A. Langen 1994, unpubl. PhD thesis, University of California, San Diego). Males disperse from their natal territory between 4 and 23 months post-fledging and circulate among other territories on reaching maturity, while virtually all females remain philopatric (Langen 1996). In this paper, I describe the mating system of White-throated Magpie-jays and evaluate Greenwood’s hypothesis as an explanation for the unusual pattern of sex-biased dispersal.

**METHODS**

**Study site and population**
I conducted this study at Santa Rosa National Park, Guanacaste Conservation Area, Guanacaste Province, Costa Rica.
(85°37'W. 10°50'N), from May to September 1990 and from April 1991 to August 1993. Throughout the study, jays were ringed with unique colour combinations. Nestlings were ringed at about 10 days post-hatching. Over 200 jays were marked in the area. Unringed birds were identified by distinctive plumage patterns (see below). By carefully recording these differences, I was able to identify all unmarked territory members in 14 groups and most “floaters”.

In this paper, “floaters” are defined as individuals which circulate through several territories and do not have a defended home range (see also the definitions in Brown 1987, Smith & Arcese 1989). The primary breeding male and female are the pair who are responsible for most breeding attempts within a group. Other group members include all birds besides the primary breeders which have residence in and defend a group territory. Secondary breeding females are other group members which make occasional breeding attempts.

Group census and survivorship

Each day that behavioural observations were made on a group (twice monthly or more frequently), I recorded the identity of all birds seen. To document group size patterns over a larger area and to detect long-range dispersal, more exhaustive counts were performed during certain periods. A team of assistants and I counted 14–28 groups per period within an area of 20 km² by slowly riding mountain bikes along fire roads until contact was made. Groups were counted before breeding commenced (January–February), during the middle of the breeding season (May–June) and after all offspring had fledged (September–October).

Annual survivorship was calculated from the number of ringed individuals which were resighted during each census. Because I have not corrected for ring loss (which was probably minimal) or emigration from the study area, these are minimum estimates. Fledgling survivorship through the first year was calculated from the day of fledging to those ringed individuals which were seen out of the nest. Data on survivorship of breeding males and females include a few distinctive, easily identified unringed individuals. In the survivorship analysis, the category “breeding females” includes all individuals who incubated eggs.

Sexing

Magpie-jays are sexually dimorphic (Goodwin 1986, Madge & Burn 1994). I found that individuals could be reliably sexed in the field using a combination of plumage characters. Males have (1) a partially white crest, (2) white between the beak and crest, (3) little or no black between the eye and the top of the head, (4) a small black auricular patch and (5) a thin, often incomplete breast-ring. Females have (1) a mostly black crest, (2) black or “pepper-and-salt” between the beak and the crest, (3) much black between the eye and the top of the head, (4) a pronounced auricular patch and (5) a thick breast-ring. In the band, males have significantly longer crests and tails. An examination of museum skins confirmed the reliability of these characters. In addition, the sex of many individuals was corroborated by the performance of sex-specific behaviour. Males perform a “dance” sexual display toward females. Breeding females produce a characteristic food-begging call and are the sole incubators.

Breeding behaviour

In 1992 and 1993, I observed breeding behaviour from the initiation of nest building to the fledging of the young. nests were observed through telescopes at a distance of 20–75 m, depending on group members’ tolerance of disturbance, for 90 min per morning. Each instance that an individual brought food to the incubating female or nestlings was recorded. The number of female food-begging calls during the sample was also noted. Occasionally, a second female group member built her own nest and attempted to breed within the territory, so I distinguished results from the nests of primary and secondary breeding females.

Statistical analyses

Parametric statistical tests were used whenever possible, and all variables were transformed as needed to meet the requirements of normality and homoscedasticity. Otherwise, nonparametric statistical tests were used. Means and standard errors are reported throughout this paper.

RESULTS

Group size and composition

Groups ranged in size from two to nine individuals over 1 year of age (mean = 5.3 ± 0.31, n = 33). The sex ratio among group members was highly skewed. There were significantly more females than males in each group (1992: paired tₐ = 7.1, P < 0.001; 1993: paired tₐ = 8.0, P < 0.001: Fig. 1). A typical group was composed of four females and one male (females: 3.9 ± 0.25, range = 1–7; males: 1.4 ± 0.11, range = 1–3).

The age composition of birds in groups was incompletely known because the life expectancy of the birds is much longer than the length of this study. For the six groups whose members were ringed early in the project, 68% of the adult members were three or more years of age by the end of my final field season. Based on resightings of ringed individuals, the estimated survivorship is 0.64 ± 0.098 per annum for the first year of life and 0.89 ± 0.044 for adult group members (age 1 year or more) in this population (Table 1).

Floaters

A large number of individuals did not associate exclusively with one group. A total of 20 floaters were detected among the nine territories that were regularly monitored during
1992

Caja 2
Aviary

Comedor
degmq

Camp
nabcdefghijkl

Casona

Cerca
eijp

Rosa Maria
bcQ

Chiringon
abcdfkl

1993

Laguna

Comedor

San Emilio

Valle
cov

Caja 2
destzA

Aviary

DEJmSPywyx

Camp

CaCDElorx

Skipper's

Cerca

djIry

Rosa Maria
cO

Chiringon
cIrx

Figure 1. Occurrences of floaters among White-throated Magpie-jay territories monitored in 1992 and 1993. Dots portray the relative positions of the territories only and not the area or length of shared boundaries. Each letter represents a different floater, and the same letter is used for the same individual between years. Small letters are used for fewer than five sightings in a territory; capital letters, for five or more sightings; capital letters with the larger font, more than ten sightings. Outlined letters are used in the natal territory of floaters. Underlining is used if a floater was observed provisioning a breeding female or offspring in a territory. Letters located outside territory boundaries represent sightings of known floaters outside of the territories that were regularly monitored.

Table 1. Survivorship estimates for the different classes of group members and floaters, based on resightings of ringed White-throated Magpie-jays

<table>
<thead>
<tr>
<th>Period</th>
<th>Survived</th>
<th>Total</th>
<th>Survivorship (mean ± s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fledglings</td>
<td>1 month</td>
<td>20</td>
<td>0.90 ± 0.081</td>
</tr>
<tr>
<td></td>
<td>6 months</td>
<td>19</td>
<td>0.76 ± 0.087</td>
</tr>
<tr>
<td></td>
<td>1 year</td>
<td>16</td>
<td>0.76 ± 0.098</td>
</tr>
<tr>
<td>Adults (all)</td>
<td>1 year</td>
<td>71</td>
<td>0.88 ± 0.037</td>
</tr>
<tr>
<td>All group</td>
<td>1 year</td>
<td>47</td>
<td>0.89 ± 0.044</td>
</tr>
<tr>
<td>members</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breeders</td>
<td>1 year</td>
<td>18</td>
<td>0.86 ± 0.078</td>
</tr>
<tr>
<td>Nonbreeders</td>
<td>1 year</td>
<td>29</td>
<td>0.91 ± 0.052</td>
</tr>
<tr>
<td>Floaters</td>
<td>1 year</td>
<td>24</td>
<td>0.76 ± 0.067</td>
</tr>
<tr>
<td>Breeding</td>
<td>1 year</td>
<td>17</td>
<td>0.85 ± 0.080</td>
</tr>
<tr>
<td>females</td>
<td>breeding season</td>
<td>11</td>
<td>0.85 ± 0.044</td>
</tr>
<tr>
<td>Breeding males</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1992, while 29 floaters were detected among the 12 territories monitored in 1993 (Fig. 1). In 1993, the minimum ages of 26 floaters were: 31% 1 year old, 54% at least 2 years old, 19% a minimum of 3 years old and 8% over 3 years old. Annual survivorship of floaters was estimated to be 0.86 ± 0.067, which was not significantly lower than group members (Table 1).

Using the plumage criteria, about 95% of floaters were males. Behavioural observations during the breeding season (e.g. attempted extra-pair copulations) revealed that a few of the remaining individuals which appeared to be female by plumage criteria had been misclassified. In another study where jays were sexed by laparotomy and breeding behaviour (K. Innes, 1992, unpubl. PhD thesis, Cornell University), 44 of 50 known-sex floaters were male.

Some floaters were rarely observed, while others were regularly detected in a subset of the monitored territories (Fig. 1). In 1993, when 12 territories were monitored, frequently observed floaters (minimum 20 observations per jay, n = 8) were detected in four territories, with one principal territory accounting for 69 ± 6.5% of observations. There were large differences in sampling effort among the 12 territories. Nevertheless, only 1 of the 11 floaters that were detected at least five times within two intensively sampled territories in
1993 was shared between them. These territories (Aviary and Casina) were only 500 m apart, and many floaters circulated among a circuit of a few territories rather than wandering more widely.

Although I often saw floaters foraging or resting alone, I regularly observed them foraging with group members without apparent aggression. Floaters aided in mobbing predators but did not participate in intergroup fights. They occasionally preened group members. Floaters typically associated with a group for only part of a morning and joined and left groups independently of other floaters.

Although floaters were frequently observed near nests when breeding females were present (see Mating and egg laying, below), they rarely provisioned nests (proportion of nest provisions = 0.03 ± 0.003). They were also primarily responsible for the few provisioning “mistakes” that were observed. Individuals that brought food and then refused to feed the female or nestlings were floaters in 6 of 11 instances. In 10 of 11 instances, individuals that brought inappropriate items such as sticks or leaves to nestlings were floaters. Floaters were responsible for far more of either type of mistake than would be expected by the number of times they provisioned ($\chi^2 = 93, P < 0.001$).

Sex and breeding ratios

Among the 12 territories in 1993 for which the total numbers of group members and floaters were known, 50 female and 17 male group members were present. Of the 50 females, 19 attempted to breed as primary or secondary breeders. Assuming that nearly all floaters were male, about 46 males were present in the population. Therefore, the ratio of males:females was not significantly different from 1:1.

Mating and egg laying

A total of 13 copulations were observed during the study: eight between a breeding female and a group male, two between a breeding female and a floater male, and three between other group members and floater males. Copulations between the group male and primary breeding female occurred at the nest from 4 days before incubation to 2 days after. No more than one copulation was observed during any morning focal sample. Each of the two cases where the breeding female mated with a floater occurred during the second week of incubation at the nest. Helpers (secondary breeders) mated with floaters away from the nest.

From the time nest building began, the group male followed the female as she collected nest material or perched in a conspicuous location as she begged near the nest. From nest building to about the second day of incubation, I observed the male in sight of the female 90 ± 2.3% of the time ($n = 33$ focal samples). During the remaining 10%, the male may have been in sight of the female but was not detected by me. Floater males were attracted to the breeding female during this period, probably by the loud, repetitious begging calls broadcast by her (see below). For 11 90-min nest-watches where all floaters were identified, 3.6 ± 0.51 floaters, with a maximum of six, were aggregated near the nest. The breeding male chased floaters 1.4 ± 0.22 times per hr ($n = 48$ observation periods). Typically, floaters would perch at a distance from the female and, if the male was away feeding or chasing another male, would fly directly to her and try to provision and perform the mating display. Female responses included accepting the food, soliciting a mating and giving a vocalization which caused the male to return and chase the floater. The guarding male usually did not chase floaters unless they approached the female. When group members approached with food, the male sometimes begged like the female, and this often resulted in the male being fed.

While building the nest and during the period she was laying but before full-time incubation had started, the breeding female produced loud “begging” calls (calls similar to fledgling begging which elicit provisioning behaviour from other group members and floaters) which were detectable over 100 m. This calling peaked during the last few days before incubation, then rapidly declined in frequency after incubation began (begs/hr; pre-incubation = 204 ± 17.9, incubation = 30 ± 4.3). For short periods, one or two other female group members might beg within hearing range of the nest. Egg laying began during this period, and incubation did not begin until about the laying of the penultimate egg. While laying but before incubating, the breeding female performed behaviour which suggested that she was not guarding; she remained almost exclusively in the vicinity of the nest throughout the day, and she flew to the nest and sat on it if any bird approached.

I witnessed 28 aggressive interactions between the breeding female and other individuals near the nest. In six instances, floater males tried to climb onto an incubating female and were repulsed. In 16 instances, the aggression was directed at another female. In all six instances in which the female could be identified, she was a group member. I regularly observed group females that appeared to be skulking and waiting for the breeding female to leave the nest. For example, a 3-year-old female that had been "resting" for 30 min flew 50 m directly to the nest and sat after the breeding female (her mother) and her mother's mate flew off forage. She was detected within 2 min; the breeding female landed on her back, bit her and both tumbled out of the nest to the ground. The daughter then flew off. In other instances, I observed females attempting to drive the breeding female off the nest. Frequently, the breeding male assisted in chasing them off. I observed females try to get access to the nest up to three times in a morning. The longest period that an intruder female remained on a nest was 6 min, but in one case I followed a breeding female away from the nest for 17 min to find a female sitting on the nest upon her return.

Circumstantial evidence suggests that female group members tried to "dump" eggs into the primary breeding female's nest. Clutch size increased with the number of females in a
group (Fig. 2). The larger clutch sizes were much larger than the typical four or five eggs reported for most New World jays in Goodwin (1986). More direct evidence of dumping came from one case in which a female aggressively displaced a female that had already begun to incubate a full clutch. This case was somewhat aberrant because the nest was built by a secondary breeding female, while the intruder was another member of the group but not the primary breeding female. The primary breeding female's nest had failed, and other group members had switched to provisioning this secondary female's nest. The intruding female laid a second clutch in the nest. The eggs from the first clutch hatched and the eggs of the second clutch subsequently disappeared. Although females appeared to carefully examine the nest contents after an altercation, I never witnessed egg removal or infanticide.

Only the breeding female incubated. Breeding females incubated nearly continuously, but short breaks were taken throughout the day. During the incubation stage, the breeding male nest-guarded while she was away (89 of 95 recorded instances). After the eggs had hatched, all group members participated in guarding the nest (the male guarded 140 of 345 instances). The difference in guarding patterns between the two stages was highly significant ($\chi^2 = 81.9$, $P < 0.001$).

Female jays built a new nest and laid a replacement clutch about 1 week after a nest had been destroyed (Fig. 3). The breeding season was long, beginning in February and lasting into July. Because nest failure was frequent (probability of nest failure = 0.72 ± 0.052, $n = 75$) and because the breeding season was long, several nest attempts were made by a group during a season (mean nest attempts: 3.7 ± 0.27, maximum = 6, $n = 14$). The cycle of failure and renesting led to asynchronous breeding among groups (Fig. 3).

Secondary breeders

In 9 of 17 group-years, a second female attempted to nest within the group territory during the breeding season. Such
females made one or two attempts in comparison with many attempts by the primary breeding female (Fig. 3). Secondary breeders or their offspring were provisioned significantly less by other group members if the primary breeder had an active nest (preincubation: $F_{1,9} = 13.9, P < 0.001$; incubation: $F_{1,4} = 25.3, P < 0.001$; nestlings: $F_{1,11} = 8.5, P < 0.005$). The failure rate of secondary nests was not significantly different from that of primary nests in the area (one of nine secondary nests successful, 12 of 51 primary nests successful; Fisher’s exact test, n.s.). Nevertheless, if a secondary breeder’s nest was still present when the primary breeder’s nest failed, group members switched to helping the secondary breeder.

In two cases, floaters were observed associating with secondary breeding females during the preincubation period. Unfortunately, too few secondary breeding attempts were monitored during the preincubation period to estimate what proportion of secondary clutches were fathered by floaters v resident males.

I observed some piracy of nest material but not aggression by primary breeders toward secondary breeders. Although secondary nests were usually not located near a primary breeder’s nest, I did find cases where secondary nests were close enough for the primary breeder to have been able to detect them visually. It appeared that the primary breeding female tolerated occasional nesting by group members. The number of attempts that were made by secondary breeders may have been limited because they received little assistance from other group members.

Replacement of breeders

I observed one instance of replacement of the primary breeding female after her disappearance. She was replaced by a secondary breeding female in the group. Because group members switched to provisioning secondary nests if the primary nest failed, I suspect that primary breeding females are usually replaced by secondary breeders if one is present.

In the two cases where I observed the natural disappearance of a primary group male, both were replaced by floater males. During one of these events, one floater had tenure for about 3 weeks until permanently replaced by another. Both floaters had been observed in the territory before the primary male’s disappearance.

During the 1993 breeding season, I removed the Casona group male for a period of 3 days. He was immediately replaced by a floater ( floater A in Fig. 1). When the group male was liberated, he immediately returned to mate guarding. I did not observe any elevated level of aggression between the floater and the male after his return, but the floater no longer approached the female and began circulating among other territories within a few days.

DISCUSSION

White-throated Magpie-jay groups consist of undispersed offspring of both sexes, related adult females and one male recruited from outside the group. Replacement primary breeding females are probably recruited from within the group. Male offspring disperse during their first or second year and float among a circuit of territories until joining a group as a breeding male.

During breeding, intrasexual reproductive competition was apparent. Male breeders prevented floaters from approaching the primary breeding female. The primary breeding female prevented access to the nest by other females during egg laying and incubation. Some female group members attempted to dump eggs or to nest within the territory. All females within the group, however, assisted the primary breeders’ reproductive efforts by feeding the female and offspring (Langen 1996).

Sex-biased dispersal and the mating system

Greenwood (1980) suggested that the difference in the sex bias of natal dispersal between mammals (males disperse more) and birds (females disperse more) is not due to phylogeny. Instead, the mating system drives the direction of the bias. If males defend resource territories, females are the dispersing sex, but if males defend females, then males disperse more. Since males of most bird species defend resource territories while males of most mammal species defend females, a phylogenetic association results. Greenwood reported patterns of dispersal in a few species of mammals where males defend resource territories and in birds where males defend females. These cases appear to support his hypothesis. As he pointed out, more exceptional cases need to be documented to determine whether the association between mating systems and dispersal, regardless of phylogeny, is as strong as it appeared when he made his review (see Arcese 1989 for another perspective).

Comparing Greenwood’s summary of the main features associated with mating systems and dispersal and the results of this study, I find a striking concordance with his predictions (Table 2). Although group male White-throated Magpie-jays do participate equally in territorial defense along with other group members, their primary reproductive strategy is to defend mates. Probably the resource territorial system evolved from traditional male resource defense to the current system because of the dispersion of resources (T.A. Langen, 1994, unpubl. PhD thesis, University of California, San Diego). Now, females defend territories along with the male. Males have switched from territory defense to attract mates to defense of females on shared territories. The White-throated Magpie-jay has a mate defense mating system and, as predicted by Greenwood, males are the dispersing sex. The main difference between Greenwood’s characterization of a mate defense mating system and that of the White-throated Magpie-jay is that primary breeders are socially monogamous pairs. Genetic paternity analysis may, of course, show that the primary breeding system is more complicated since either sex may potentially have multiple partners.

I suggest that males disperse and females remain philo-
Table 2. A comparison of the main features of mating systems and dispersal in birds and mammals (from Greenwood 1980: table V) and the results of this study

<table>
<thead>
<tr>
<th>Resource defence (mainly birds)</th>
<th>Mate defence (mainly mammals)</th>
<th>White-throated Magpie-jay</th>
</tr>
</thead>
<tbody>
<tr>
<td>High male investment in resources in presence or absence of mate(s)</td>
<td>Low male investment in resources, particularly in absence of mate(s)</td>
<td>Group breeding males: contribute to territory defence</td>
</tr>
<tr>
<td>Low female investment in resources</td>
<td>High female investment in resources</td>
<td>Floater males: circulate among territories</td>
</tr>
<tr>
<td>Intermale competition for resources</td>
<td>Intermale competition for mates</td>
<td>Females defend territories</td>
</tr>
<tr>
<td>Mainly monogamous</td>
<td>Mainly polygynous</td>
<td>Group breeding males: mate defence against frequent incursions by other males during female fertile period</td>
</tr>
<tr>
<td>Male philopatry</td>
<td>Female philopatry</td>
<td>Floater males: attempt to copulate with primary breeding females, court other group females</td>
</tr>
<tr>
<td>High cost to male dispersal?</td>
<td>High cost to female dispersal?</td>
<td>Group breeding males: monogamous (or polygynous?)</td>
</tr>
<tr>
<td>Greater male natal and breeding dispersal</td>
<td>Greater male natal and breeding dispersal</td>
<td>Primary breeding females: monogamous (or polygynous?)</td>
</tr>
<tr>
<td>Reproductive enhancement—female choice of male breeders</td>
<td>Reproductive enhancement—increased access to females</td>
<td>Floater males and other females: polygynandrous</td>
</tr>
<tr>
<td>Inbreeding avoidance</td>
<td>Inbreeding avoidance</td>
<td>Female philopatry</td>
</tr>
<tr>
<td>Evolution of patrilineal social organization</td>
<td>Evolution of matrilineal social organization</td>
<td>More aggression towards female breeders</td>
</tr>
</tbody>
</table>

For a female to reproduce without having a mate, she may either have a male that is not able to mate with her, or have a male that is unable to mate with her. This male could successfully resist attempts to mate with her, but it is not clear whether either sex would benefit more by having the other sex present. It is not clear whether either sex would benefit more by having the other sex present.
portion of adults (75%) are excluded from primary breeder status and opportunities to attain breeding positions are infrequent. Second, the breeding season is long and the number of nest attempts per group appears to be unusually high. A number of tropical corvids and other species appear to fit this pattern, but their dispersal pattern is poorly known. There may be a continuum in the New World jays, for example, from those in which males frequently attain territories (Florida Scrub Jays Aphelocoma coerulescens; Woolfenden & Fitzpatrick 1984, 1990), to those in which new territories rarely become available, the mating season is short but multiple females breed on the territory (Mexican Jays Aphelocoma ultramarina; Brown & Brown 1990), to those species where new territories rarely become available, few females breed on a territory but the breeding season is long and breeding attempts asynchronous (White-throated Magpie-jays: this study). In these three species, dispersal ranges from female-biased dispersal (Florida Scrub Jay), to little dispersal by either sex (Mexican Jay), to male-biased dispersal (White-throated Magpie-jay).

In addition, male-biased dispersal may not be so rare in group territorial or cooperative breeders as has been supposed. Slightly male-biased dispersal has been documented in the group territorial, pair-breeding Australian Magpie Gymnorhina tibicen (Velman 1990), the communally breeding Pukoko Porphyrio porphyrio (Craig & Jameson 1990) and a colonial population of cooperatively breeding American Crow Corvus brachyrhynchos (Caffrey 1992). Just as avian mating systems are being found to be more variable than had been previously supposed (Stacey & Koenig 1990), the direction of sex bias in dispersal may also prove to be more variable than we had once thought.

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