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Female Adélie Penguins Acquire Nest Material from Extrapair Males after Engaging in Extrapair Copulations

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Females of a number of bird species occasionally have been recorded exchanging copulations directly for food or for access to food resources (Lack 1940, Brown 1967). For example, Wolf (1975) found that male Purple-throated Caribs (*Eulampis jugularis*) defend groups of flowers from conspecifics but allow females access in exchange for copulations. Similarly, in monogamous Red-billed Gulls (*Larus novaehollandiae*), Tasker and Mills (1981) showed that a female is more likely to copulate if the male gives her food during courtship. We are unaware of any description of copulations being directly exchanged for any material item other than food. Furthermore, this behavior seems to be limited in monogamous species to within-pair interactions, with no records of females of any species trading food or any other immediate material benefit for extrapair copulations (EPCs; Birkhead and Møller 1992).

Here, we describe female Adélie Penguins (*Pygoscelis adeliae*) acquiring nest material from extrapair males after engaging in copulations with them. This material is in the form of small stones used to create a platform on which the female lays her two eggs. Stones are in great demand in the colony and are collected by both males and females from the ground in the area surrounding the breeding group (Sladen 1958). In addition, individuals regularly steal stones from the nest sites of other individuals (Sladen 1958). Any individual approaching a male at his nest site and taking a stone is met with an aggressive response from the site-holder (Spurr 1975a). Site-holders will peck, "flipper-bash," and chase stone-stealers. The benefit of collecting and defending a large pile of stones is realized under particular weather conditions, usually in springtime, when meltwater can inundate the breeding colony. Flooding by meltwater can result in nest desertion and egg loss (Taylor 1962). Moreno et al. (1995) found that in the closely related Chinstrap Penguin (*Pygoscelis antarctica*), which displays similar stone-collecting behavior to the Adélie Penguin, large nests were less likely than small nests to fail as a result of flooding by meltwater. Moreno et al. (1995) concluded that stone collecting and nest maintenance improved nest quality and increased reproductive success.

Adélie Penguins are monogamous and breed in large colonies in Antarctica. They engage in courtship and copulation behavior during the prelaying period, which spans from mid-October to the end of November (Spurr 1975b). Our study site is situated in the Northern Rookery at Cape Bird, Ross Island, Antarctica (77°13′S, 166°28′E). Observations of copulation behavior were made during the prelaying periods in 1993, 1994, 1996, and 1997. Full descriptions of the study site and methods are available in Hunter et al. (1995, 1996).

The following account is based on 10 observations involving at least five different females, seen over the four seasons of study. In each case, a female joined a single, unpaired male at his nest site; courtship (sideways-stare and bow; Spurr 1975a) was followed by the female lying prone at the male's site. The male then mounted and copulated with the female (see Hunter et al. [1995, 1996] for a full description of copulation behavior). In 8 of the 10 cases observed, copulation resulted in successful insemination of an ejaculate, determined by observation of the male's ejaculate entering the female's cloaca. In one unsuccessful copulation attempt, the male produced an ejaculate that missed the female's cloaca. In the remaining copulation attempt, the pair was disrupted by a neighboring individual prior to cloacal contact, and the male terminated the attempt. Following each copulation, the male dismounted from the female, and she picked up a stone from his nest site and left immediately. In 5 of the 10 cases, the female returned to the extrapair male forthwith to take a second stone and left again without copulating. One of these females returned a total of 10 times, taking a stone from the extrapair male on each occasion. At no time was there any aggressive response by the male; he made no move to stop the female from taking a stone from his site. Seven of the 10 females that gained stones following copulations were unbanded, suggesting that they came from outside the study group in which most of the birds were banded. This was supported by the fact that on four occasions, these females were followed after copulation and were found to have partners and nest sites in breeding groups adjacent to the study group. Each of these females returned to her partner immediately after the EPC and deposited the stone at their nest site. The remaining three females, each of which was banded, copulated and took stones from males within the study group and then returned to their partners, also in the study group. Despite a number of males engaging in EPCs at females' nest sites, in no case did a male take a stone from a female's site following an EPC.

In addition, as previously reported by Derksen

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(1975), females were observed acquiring stones from males without engaging in copulations. In each case, this behavior was initiated by the female joining an unpaired male at his site and engaging him in mutual courtship behavior. She then simply took a stone and left the site. Again, the male was not aggressive toward the female, suggesting that females may avoid aggression by soliciting courtship. Ten females were observed to engage in this behavior: one female was observed to take at least 62 stones from a single male over a period of approximately one hour; another female took one stone from one male and three stones from another male four days later; a third female took stones from a single male on two separate occasions (four days apart). The incidence of this behavior would have been underestimated because it was recorded late in the 1996 season by FMH only, and in 1997. In addition, this behavior may have been overlooked during periods of peak copulation activity because the focus of observations was copulation behavior rather than courtship behavior. In these cases, it would appear that the male was cheated into allowing the female to take a stone without gaining anything himself.

On a few occasions ($n = 7$), in response to a female attempting to steal a stone from a male's nest site, the male, instead of defending his stones, attempted to mount the female. In each of these cases, the female immediately moved away from the male and did not allow him to mount. In only three of the seven cases did the female leave with a stone. It is possible that the male misinterpreted the female's head-down posture during the process of choosing a stone and took it to be the head-bow courtship display that usually precedes copulation, although in no case did the female lie prone at the site, a necessary precursor to successful mounting.

It appears that female Adélie Penguins will sometimes acquire nest stones from extrapair males after engaging in EPCs. Various points of interest can be noted from these observations: (1) females chose unpaired males with whom to engage in EPCs (females of most species choose paired males; McKinney et al. 1984, Birkhead and Møller 1992); (2) a high proportion of the EPC attempts was successful (compared with 59%, $n = 35$ pairs, of pair copulations successful; Hunter et al. 1995); (3) the currency involved was nest material rather than food; and (4) the material benefit was gained following EPCs rather than pair copulations.

The male clearly benefits by gaining an EPC that could result in offspring fathered by him but raised by another male (McKinney et al. 1984, Birkhead and Møller 1992). The cost of one or two stones would appear to be a small price to pay for so large a potential benefit. The male also may gain if allowing a female to take a stone means that she is more likely to return for additional copulations, which could increase his chances of fertilizing her eggs. In addition, if the male is unaware of the female's status as a paired individual, he may view the copulation as the initiation of a long-term partnership, in which the female rearranging nest stones (although not taking them away from the nest site) would constitute normal behavior. Because many long-term pairings are initiated by a female coming to a male's site, courting with him and engaging in copulation, any male ignoring such a solicitation, or acting aggressively toward a female manipulating his stones, might miss a genuine opportunity to form a pair.

It is harder to see what a female would gain from trading an EPC for one or two stones. A straight exchange would suggest that to the female, either the two were equally valuable, or the EPC was less valuable. This seems unlikely when an EPC has the potential to alter the paternity of her offspring, whereas a single stone does little to increase the likelihood of a successful breeding attempt. It is possible that the exchange of one EPC opens the way to the female to collect multiple stones, which might indeed increase the chances of her offspring surviving. If so, the pair male might be predicted to respond to his female engaging in extrapair copulations by attempting to collect enough stones to prevent his female from needing to steal them. Alternatively, a female may engage in an EPC for some other reason (e.g. fertility assurance, increasing the quality of her offspring, gaining a potential future partner; Westneat et al. 1990) but then exploit the male's lowered guard by taking a stone after she has engaged in the EPC. In this scenario, the female gains both an EPC and some easily obtained nest material. In addition, by returning to her pair male with a stone, she may be supplying him with a reason for her absence. This trickery would benefit both the female and the extrapair male if it reduced the chances of the pair male attempting a retaliatory copulation (Birkhead and Møller 1992).

In conclusion, it appears that female Adélie Penguins sometimes acquire nest material from extrapair males after engaging in an extrapair copulation, and that both female and extrapair male gain from this behavior. Even the female's pair male gains a stone in his nest, although this particular stone and the others in his nest ultimately may help to protect the life of an offspring that is not his own.

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"Wife-sharing" in the Tasmanian Native Hen (*Gallinula mortierii*): Is it Caused by a Male-biased Sex Ratio?

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In many cooperatively breeding species of birds, adult males are thought to outnumber adult females (e.g. Red-cockaded Woodpecker [*Picoides borealis*], Gowaty and Lennartz 1985; Splendid Fairy-Wren [*Malurus splendens*], Rowley and Russell 1990; Pied Kingfisher [*Ceryle rudis*], Reyer 1990; see Emlen 1984, Brown 1987). The occurrence of male-biased sex ratios in some populations of species with helpers-at-the-nest has led to the hypothesis (the differential mortality model of Emlen et al. [1986]) that a shortage of females could explain—at least in part—delayed dispersal, helping behavior, and mate-sharing by males (Rowley 1965, Maynard Smith and Ridpath 1972, Emlen 1984, Curry and Grant 1989, Reyer 1990, Davies 1992). A shortage of females might result from a higher rate of mortality compared with males, perhaps associated with female-biased dispersal. An experimental test on Superb Fairy-Wrens (*Malurus cyaneus*) provided support for this model (Pruett-Jones and Lewis 1990).

A classic example in the debate on the link between sex ratios and cooperative breeding is the Tasmanian Native Hen (*Gallinula mortierii*). Ridpath (1972b) reported male-biased sex ratios among both adults (1.5 males per female) and chicks (2.8 males per female) in his study population, and an overall sex ratio of 1.22 males per female among 489 individuals collected near his study area and sexed by dissection. Maynard Smith and Ridpath (1972) used

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