steroid measurements to the assessment of gonadal activity in free-living Kakapo. The survival of this endangered species depends on egg laying by female Kakapo. Thus, conservation efforts are focussed on the females. The shortage of female samples in our study means that further sample collection programs are needed to realize the potential of this new method to provide information on the reproductive condition of female Kakapo. In a wider context, fecal steroid measurements can now be applied to other free-living birds for which handling and blood sampling is difficult or inappropriate.

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Polygyny in the Asian Openbill (*Anastomus oscitans*)

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Although monogamy is the predominant mating system in birds, there are few strictly monogamous bird species (see review by Ford 1983). Other than the widespread occurrence of polygyny in various species, occasional polygyny also has been reported in normally monogamous species (Armstrong 1955, Verner and Willson 1969, Logan and Rulli 1981, Marks et al. 1989). Although Brown (1987) did not include any members of the Ciconiiformes in his list of 222 species of communally breeding birds, occasional polygyny also has been found in this group (Lancaster 1970, Cramp 1977, Fujioka 1986, McKilligan and McConnell 1989). However, storks always have been found to breed monogamously (Ali and Ripley 1968, Cramp 1977, Coulter et al. 1989).

We describe several cases of polygyny in a breeding population of a stork, the Asian Openbill (*Anastomus oscitans*). We also report information concerning the formation of such mating groups and the success experienced by them in comparison to monogamous pairs.

Methods.—Our study was conducted at the Raiganj Wildlife Sanctuary (25°36′N, 38°10′E), West Bengal, India, where Asian Openbills are found breeding from July through December, as are five other waterbird species.

We studied this population of openbills from 1987 to 1991. Nests with more than two adult birds were considered as a possible case of polygyny, and we kept close watch on those nests. Data from those nests

were taken into account only when the presence of more than two adult birds was confirmed by direct observation for at least three consecutive days.

Members of 37 such groups were color marked with nontoxic textile dyes using a sprayer from a high vantage position above the nest-rim level. For each nest we maintained an identity card with the records of the position of the nest in the sanctuary and the marking patterns or identifiable physical traits of the members. Sexes were ascertained from behavior. Position during copulation was treated as a good indicator of sex, as "reverse mounting" is very rare in this species. Above all, we think our continuous and careful observations were effective in making certain that we did not introduce the confounding effect of reverse mounting.

Nests were inspected each day before hatching and thereafter on alternate days. Observation was made from a high vantage position or from the ground with minimum interference to birds in the area. To compare success rates, four monogamous pairs were selected as controls for each polygamous nest. Control nests were selected from the close vicinity of the polygamous nest; the physical and breeding statuses of all control birds were similar. Observations were made with the naked eye or with $20\times$ binoculars. Measurements of eggs were taken with a vernier caliper, and masses of young were taken with a Pesola spring balance.

Results.—During this five-year study, we found 51 monogamous groups of 2,115 active nests. In 2 cases, four birds used a single nest, and the other 49 nests were occupied by trios.

In this colony, openbills usually started nesting from the first week of July. The polygamous nesting attempts were not seen until August, when almost all of the nesting trees were invaded by monogamous pairs. Nesting by monogamous pairs also continued until the last week of September. After the third week of July, most of the new settlers had no option other than to choose a preoccupied nesting tree for nesting, which often resulted in intraspecific fighting. Naturally polygamous groups always nested in a preoccupied nesting tree with many monogamous nests. Polygamous nests were not confined to any particular zone of the colony, but were scattered throughout.

Copulatory behavior confirmed the sexes of the members of 21 trios in which two females mated with a common male. In 15 other cases, behavioral (other than copulation) and physical characters of the members also suggested that only one male was involved. However, for the remaining 15 cases, sexes of the members of those mating groups were not identified.

We witnessed the formation of such mating groups on seven occasions. It was a direct consequence of intraspecific attack. In each case the unattached bird made an attack on an already mated monogamous pair with a four- to seven-day-old nest. The resulting fight attracted other unattached birds of the colony, which

rushed to that spot and got involved in the disturbance. In these cases, fighting continued for 5 to 18 min ($\bar{x} = 588 \pm$ SD of 296.74 s), involving 6 to 13 birds ($\bar{x} = 9.29 \pm 2.29$). The duration of fighting was directly proportional ($r = 0.946$) to number of birds involved. At the end of fighting, three or four birds were found to rest peacefully in that nesting spot. The new group sometimes included one or both of the original pair, but this was not always the case. Within a very short period, the birds at the nest made joint up-down displays (Kahl 1972) in very close succession. Thereafter, they behaved as a unit in all respects, exhibiting pair-forming displays, as done by monogamous pairs. Such intraspecific attacks were very common in this colony and, in most cases, they ended with only two birds in the nest.

We were able to survey the development and success of clutches at 11 polygamous nests. Polygamous clutches showed greater variation in laying order than those in monogamous nests, where eggs were consistently laid on alternate days. In polygamous nests, most of the eggs were laid on alternate days; however, in six instances eggs were added to the clutch on the same day. In another nest, there was a three-day interval between eggs. Clutch size of polygamous nests ($\bar{x} = 4.45 \pm 1.44$, $n = 11$) was significantly higher ($t = 3.76$, df $= 53$, $P < 0.001$) than that for the control monogamous nests ($\bar{x} = 3.41 \pm 0.54$, $n = 44$).

Intraclutch variation of egg dimension did not follow definite order in polygamous clutches, in contrast to the situation in monogamous clutches. In monogamous clutches, larger eggs always were laid in the middle of the clutch. In three- or four-egg clutches, the second egg was largest, while in five-egg clutches the third was largest. In polygamous clutches, no such order was maintained and, in some cases, the first or last egg of the clutch was the largest. Intraclutch differences between the largest and smallest egg were significantly greater in polygamous nests ($t = 3.76$, df $= 53$, $P < 0.001$). In 44 control monogamous clutches, the range of egg volumes was never more than 30% ($\bar{x} = 14.8\%$) of the smallest egg volume. However, in 8 of 11 polygamous clutches, this difference was more than 35% ($\bar{x} = 30.6\%$).

Hatching success and fledging success were considerably higher in polygamous nests, while loss due to intraspecific attack was higher in monogamous nests (Table 1). The mass of young birds at fledging was significantly higher ($t = 3.2$, df $= 49$, $P < 0.005$) in polygamous nests.

All members of the polygamous nests shared in most of the parental activities, from nest building to food provisioning of young. We saw no obvious signs of parental discrimination in these polygamous groups. As a result, the whole clutch or brood received more care than did those in monogamous nests. During the egg stage, more than one parent attended the polygamous nest for more than 85% of daytime hours (316.5 h of 360 h observed), while this occurred

TABLE 1. Reproductive success in polygamous and control monogamous nests (*n* in parentheses).

	Hatching success (%)	Fledging success (%)	Loss due to intraspecific attack (%)	Mass at fledging (g; $\bar{x} \pm$ SD)
Polygamous	77.6 (11)	89.5 (11)	5.0 (40)	1,279.8 ± 78.7 (21)
Monogamous	66.0 (44)	81.8 (44)	15.9 (44)	1,208.2 ± 76.0 (30)

only 40% of the time during the day (375.1 h of 926 h observed) at monogamous nests. Before hatching, the total time when birds were not incubating a nest during daytime hours was significantly higher (t = 11.7, df = 53, P < 0.001) in control monogamous nests ($\bar{x}$ = 121.8 ± 11.2 min) than in polygamous nests ($\bar{x}$ = 93.5 ± 7.3 min). These factors probably make the polygamous nest more resistant to intraspecific attack. None of the polygamous nests observed were destroyed completely by intraspecific attack, but 2 of 44 control monogamous clutches were destroyed completely for this reason.

Discussion.—In this sanctuary, polygamous nests were found in all the years studied. All members of such groups have been found to take active part in breeding, and the data suggest that more than one female laid eggs in a given nest. The reasons for these conclusions include: (1) in each of these groups, a single male was found to copulate with the other two members of the group; (2) larger clutch sizes seem to be the result of laying by more than one female; (3) the laying sequence was abnormal, particularly with the laying of two eggs in one day; (4) the abnormal intraclutch variation of egg dimensions relative to laying sequence seems to be due to asynchronous laying by more than one female; and (5) the greater intraclutch differences between smallest and largest egg volumes may be due to laying by females of different physical status.

From direct observation, it was evident that these mating groups formed as a consequence of fighting to establish sole dominance. Probably none of the females was dominant to the point that it could displace or chase off other females. The choice to share a nest could be advantageous because continuation of fighting is likely not only to be expensive energetically but also could attract other unattached birds, which may jeopardize the former attacker's chance of winning. However, if two or three of these females jointly stand against intruders, the result could significantly increase the fitness of the defending birds.

Mating polygynously is disadvantageous to females because of heavier predation pressure and poorer food condition (Verner 1964, Orians 1969), or due to lack of male assistance (Martin 1974, Smith et al. 1982). In Japanese Wagtails (*Motacilla grandis*), polygynous nests had a higher frequency of unhatched eggs (Nakamura 1985). However, in the case of the openbills, polygynous nests were less vulnerable to intraspecific attack, and both hatching and fledging

success were higher than found for monogamous nests. Although productivity (number of young) per female of a polygynous nest looks to be slightly lower than that of a monogamous female, quality (as reflected in fledging mass) of the young of polygynous nests was greater than that of monogamous nests. Moreover, polygynous nesting reduced the probability of total reproductive failure due to intraspecific attack. Such failure was very common at the monogamous nests, particularly in the later part of the breeding season.

In the situation we studied, the effect of territory quality (Verner 1964) or female-biased sex ratio (Emlen and Oring 1977) seems to be less significant; polygynous nests were distributed throughout the sanctuary and replacement of nesting males by new ones during intraspecific fighting or establishment of monogamous pairs up to the last week of September suggests the abundance of unattached males. Probably, scarcity of suitable nesting sites was the causal factor of intraspecific attack by unattached birds on nested pairs. Joint nesting by female Asian Openbills seemed to be an effective device to withstand the menace of intraspecific attack with no major loss in productivity.

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Water and Energy Limitations on Flight Range

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Carmi et al. (1992) proposed a computer model that furthers our knowledge of whether energy or water are the greater physiological limitation to bird flight range. With the trans-Sahara migrating Willow Warbler (*Phylloscopus trochilus*) as an example, the model is a major theoretical effort to identify several important parameters on which migratory research should be focused in the future. However, there is a shortcoming in the model, as it calculates the flying bird's energy and water budget largely independent of each other. Only the calculated energy-consumption rate in the energy budget part of the model is passed to the water-budget component for the calculation of respiratory water loss and metabolic water production. However, the usual negative water balance, as pointed out by Carmi et al. (1992), will result in a decrease of body mass that should be accompanied by changes in optimal flight speed and costs of flight. Thus, water and energy budgets influence each other mutually.

I adjusted the model by Carmi et al. to account for this continuous change in body mass due to water loss (in their energy-budget part, Carmi et al. used Pennycuick's [1989] flight-range model, which already accounts for mass loss as a result of use of energy reserves underway). In the alternative "extended" model, where the energy and water budgets of the flying bird are closely linked, the model's parameter values change continuously during flight performance. To approximate these continues changes, all parameters were evaluated and actualized at 15-min flight intervals. In this commentary, I will discuss some of the major discrepancies that occur between the original model of Carmi et al. (1992) and the extended model outlined above.

For this comparison, in concordance with Carmi et al.'s paper, I simulated the flight of a small Palaearctic passerine, the Willow Warbler (with a wingspan of 0.17 m and an initial body mass of 10 g, including 5 g water [of which a 30% loss is tolerated] and 3 g fat), during its annual migration over the Sahara desert. When not stated otherwise, a flight altitude of 2,000 m, an air temperature of 14 °C, and an oxygen-extraction coefficient of 0.039 are assumed, all in accord with the parameter settings used by Carmi et al. (1992).

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