# PRELIMINARY OBSERVATIONS ON THE OCCURRENCE AND EVOLUTION OF POLYANDRY IN THE GALAPAGOS HAWK (*BUTEO GALAPAGOENSIS*)

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ABSTRACT.—The Galapagos Hawk (*Buteo galapagoensis*) has a polyandrous mating system. We prefer to call it cooperative polyandry, because one to four males mate with a single female and all males aid in caring for the eggs and young. Preliminary observations over a 2-yr period revealed that polyandrous groups did better reproductively, on the average, than monogamous pairs (2.0 young/nest vs. 1.0 young/nest), but polyandrous males, on the average, did worse than monogamous males (0.6 young/male compared to 1.0 young/male). Polyandrous groups appeared to be highly stable in composition. The occurrence and frequency of polyandry, however, varied considerably among islands. We suggest that the frequency of cooperative groups depends upon the extent of habitat not suitable for breeding. Islands with large amounts of nonbreeding habitat supported large nonbreeding populations of hawks. Excess males provide the material and pressure for group formation. As territorial birds have a higher survivorship than nonterritorial birds (85% over 2 yr compared to 40%), polyandry is likely adaptive because the increase in life-span and thus the number of reproductively active years compensates polyandrous males for the decrement in number of young produced per breeding attempt. *Received 16 October 1979, accepted 18 February 1980.*

MOST cooperative breeding systems occur in response to some limiting condition, typically a shortage of territories or breeding sites but potentially also a shortage of mates (Woolfenden 1975, Brown 1978, Emlen 1978, Gaston 1978). Limits on available resources keep populations small, philopatric, and isolated. In addition, cooperative species often share diagnostic characteristics of K-selection, further increasing competition and thus limitation (Brown 1974). Accordingly, most avian cooperative units consist of a monogamous pair and a variable number of related, nonbreeding juvenile helpers (Brown 1978).

Not all species, however, follow this pattern. Some species form communal nests attended by a variable number of potentially breeding adults. These communal nesting attempts can be by groups of monogamous pairs, e.g. the Groove-billed Ani (*Crotophaga sulcirostris*) (Vehrencamp 1977); by groups of promiscuous individuals, e.g. the Noisy Miner (*Manorina melanocephala*) (Dow 1977) and possibly several bee-eater (*Merops*) species (Fry 1972, Emlen 1978); or by a single polygamous group, e.g. the Tasmanian Native Hen (*Tribonyx mortierii*) (Ridpath 1972), the Harris' Hawk (*Parabuteo unicinctus*) (Mader 1975a, b; 1978; 1979), and the Galapagos Hawk (*Buteo galapagoensis*) (de Vries 1973). Potentially, then, several pathways exist for the evolution of cooperative breeding.

De Vries (1973, 1975, 1976) first detailed the natural history of the Galapagos Hawk and described the occurrence of multiple-male breeding groups in this species. Because all males in the group copulate with the female throughout the breeding season, the system may be classically defined as polyandry. Because males also share

TABLE 1. Frequency and size of polyandrous groups in 1979.

|  | Santiago | Santa Fe |
|---|---|---|
| Number of breeding groups sampled | 16 | 16 |
| Number of polyandrous groups | 14 | 8 |
| 2-male groups | 8 | 5 |
| 3-male groups | 3 | 3 |
| 4-male groups | 1 | 0 |
| 5-male groups | 1[a] | 0 |
| Mean number of males per polyandrous group | 2.6 | 2.4 |
| Mean number of males per territory | 2.3 | 1.7 |

[a] This group had two females.

in incubation, defend a group territory, and provide food for the female and a single set of young, however, we suggest that "cooperative polyandry" is a more appropriate term for the mating system. This distinguishes it from serial polyandry, in which a female lays a clutch of eggs for several males in sequence (Oring and Knudson 1972, Pitelka et al. 1974), and simultaneous polyandry, in which a female may lay a clutch of eggs for several males living in subdivisions of her territory (Jenni 1974). These types of polyandry do not involve cooperative behavior and may best be explained as adaptations to temporally fluctuating resource levels (Graul et al. 1977). As the Galapagos Hawk offers such a distinctive social system and unusually good study conditions, we have initiated new field work on it. Some preliminary results are reported here.

STUDY AREAS AND METHODS

The Galapagos Islands are located on the equator some 960 km west of Ecuador. For our preliminary work we selected two islands of different topography and, thus, ecology. Isla Santa Fe (Barrington) is a small (2,413 ha), low (239 m maximum elevation) island that was formed by the uplift of submerged volcanic activity. It is covered with arid vegetation dominated by *Bursera* and *Opuntia*. In contrast, Isla Santiago (James) is the result of a large, emergent volcano. It is large (58,464 ha) and high (914 m), with many vegetation types ranging from *Bursera-Opuntia* woodlands in the lowlands through cloud forest to grasslands on the summit. A large area of the island is covered with bare lava deposited in recent times.

The climate of the Galapagos Islands, summarized by Harris (1974), consists of two seasons, generally termed "hot" and "cool." These are influenced largely by the effects of the interplay between the cold Peruvian current and warmer water from the north. Rainfall is erratic, particularly in low areas. No rainfall records are available for our study areas.

We censused and observed birds on all of Isla Santa Fe. On Santiago, our activities were concentrated in two areas. The Sullivan Bay region in the northeast corner of the island is a low, arid area with much bare lava. Most hawks observed here lived in vegetated volcanic cones that emerge from the more recent lava flows. From our camp at Bucaneer Bay in the northwest part of the island, we observed birds from the lowlands to the island's summit. This part of the island is generally wetter and more heavily vegetated. We visited Santa Fe on 23–28 July 1977 and 5–14 June 1979, Sullivan Bay on 1–7 August 1977 and 22–28 May 1979, and Bucaneer Bay on 8–12 August 1977 and 28 May–4 June 1979.

We spent most of our time searching for nests and observing breeding groups. Size and composition of groups were recorded, and territorial boundaries were plotted whenever possible. In 1977 territorial birds were captured, measured, and banded using a balchatri with rats for bait. On Santiago, we also used goat carcasses to attract and capture nonbreeding birds. In 1979 both methods of capture were tried, but, because of apparently abundant natural food supplies, neither technique was very successful.

Females are significantly larger than males, allowing separation in the field. When determining group composition, we used the largest number of males observed in cooperative or social behavior. In most
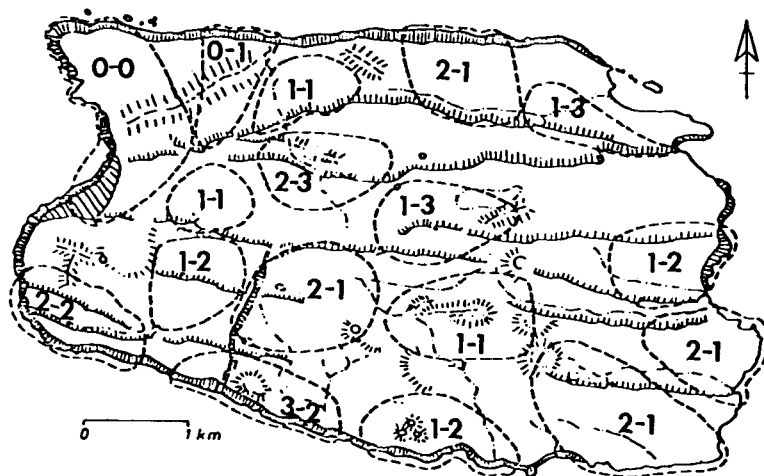
Fig. 1.   Territories of breeding hawks on Santa Fe and the number of males in each territory in 1969 and 1979.

cases, particularly in the vicinity of an active nest, all adult birds aid in defense and are readily observable. In a few cases where groups were not actively breeding, it is possible that our counts of males were minima.

Unpublished data of de Vries are also presented here. These were gathered during a 7-yr period, with field work concentrated on Isla Santa Fe. Previously published data gathered during this time appeared in de Vries (1973, 1975, 1976).

## RESULTS

*Frequency of occurrence and stability of polyandrous groups.*—Isla Santiago had nearly twice the frequency of multiple-male groups and somewhat larger group sizes than those found on Santa Fe (Table 1). One territory on Santiago had five males and two females, the first record of such a group for the Galapagos Hawk. Of the two females, one was dominant and aggressive, leading the males in attacks when we approached the nest. The second female shaded the three young or sat near the nest but rarely assisted in nest defense. We cannot assume that both females contributed eggs to the nest, however, as de Vries occasionally found single-female nests with three-egg clutches.

Although no quantitative measurements of territory quality were made, we saw no obvious relationship between any habitat parameters and group size. Territories censused in 1969 and again in 1979 on Santa Fe had relatively constant territorial boundaries, but the number of males in each territory varied (Fig. 1). The exceptional group of seven adults and three nestlings on Santiago existed on one of the smallest vegetated areas of any group observed. Just to the north of this group was a monogamous pair whose territory consisted of three or four times as much vegetated area.

Members of five breeding groups were banded on Santiago in 1977. We were able to check band numbers of four of these groups in 1979. A two-male and three-male group were still intact after the 2-yr interval. One territory containing a monogamous pair in both years had the same female but a different male in 1979. When the

TABLE 2. Estimated adult sex ratios on Isla Santiago.

|  | 1977 | | 1979 | |
|---|---|---|---|---|
|  | Males | Females | Males | Females |
| Number of breeding adults[a] | 115 | 50 | 115 | 50 |
| Number of nonbreeding adults[b] | 4 | 74 | 5 | 33 |
| Total | 119 | 124 | 120 | 83 |

[a] From sex ratios of surveyed territories multiplied by the estimated number of territories on the island.
[b] From counts of nonbreeding birds at a goat carcass.

territory containing two females was studied in 1977, five males were captured with one juvenile; no females were observed. In 1979, four of those males were still on the territory along with one new male. Thus, of 14 identifiable birds, 12 were still on the same territory in 1979. It appears that polyandrous groups generally are very stable and that birds tend to remain on their territories from year to year.

*Sex ratios and total population sizes.*—While surveying the islands, we made a special effort to look for juvenile or nonbreeding adult birds. These birds live in areas not included in breeding territories, areas that are very limited on Santa Fe (Fig. 1) but that include the extensive highlands of Santiago. De Vries (1973) observed that parents expel their offspring from the territory within 3–5 months after fledging and that juvenile birds spend the nest 2–3 yr (minimum) in nonterritorial areas.

In 1977 we captured 12 nonterritorial juvenile birds on Santa Fe and are confident that there could have been only 1 or 2 more on the island. Of these, seven were males and five females. In 1979 only 1 juvenile bird was banded, and a population size of only 4 or 5 juveniles was estimated. While the appearance of a baited trap almost immediately attracted 8–10 juvenile birds in 1977, only 2 juvenile birds were ever seen together in 1979. No certain observations of nonterritorial adult birds were made on Santa Fe in 1977 or 1979, so the adult sex ratio was the sex ratio of the breeding groups (27 males and 16 females in 1979). Thus, on Santa Fe the existing pool of nonbreeding hawks was small and largely juvenile.

Overall population sizes and sex ratios on Santiago were very different from those on Santa Fe (Table 2). During two sampling periods in the highlands in 1977, we banded 56 hawks and estimated that number to be one-half of the nonbreeding population. No banding was allowed in 1979, but a goat carcass attracted nearly 100 birds, with about one-third of those being adult females. Previous bandings have revealed varying populations of adults and juveniles, the variation apparently depending upon time of year and previous breeding success. It appears that a pool of at least 30 and up to 75 adult females was always present, however. A few banded adult females that were at least 10 yr old have been seen among these birds.

Although we were not able to survey all territories on Santiago, we are able to estimate breeding adult sex ratio. Santiago has an estimated 50 hawk territories (de Vries 1973). At 2.3 males per territory plus a few nonbreeding adult males in the highlands, there were an estimated 115–120 adult males on the island. Only by adding the largest estimate of nonbreeding adult females to the 50 territorial females do we get an equal adult sex ratio. The occurrence of such large numbers of nonbreeding adult females, however, suggests that a lack of available mates was not the important force in the evolution of polyandry in the Galapagos Hawk.

*Breeding success of pairs and groups.*—Our preliminary observations of breeding

TABLE 3. Breeding success of nests observed on Santiago, 1979, and on Santa Fe, 1969–1975.

|  | Polyandrous | Monogamous |
|---|---|---|
| SANTIAGO | | |
| Number of nests observed | 6 | 2 |
| Mean number of young per nest | 2.0 | 1.0 |
|    Nests with 1 young | 2 | 2 |
|    Nests with 2 young | 2 | 0 |
|    Nests with 3 young | 2 | 0 |
| Mean number of young per male | 0.67 | 1.0 |
| Total young produced | 12 | 2 |
| SANTA FE | | |
| Number of nests observed | 12 | 17 |
| Mean number of young per nest | 1.25 | 1.35 |
| Mean number of young per male | 0.62 | 1.35 |
| Total young produced | 16 | 23 |

success showed great variation between the 2 yr of study. In 1977, dry weather resulted in no production of young in all territories checked on Santa Fe. Birds on Santiago had better success: 5 groups that were closely observed and another 8–10 that were checked casually all produced 1 juvenile offspring each. This was true regardless of group size.

Very early rains in 1979 resulted in earlier breeding than normal on both islands. On Santa Fe, only three juvenile birds were found still with their parents. Two of these were from two-male groups, while one was from a monogamous pair. Nesting was less synchronous and generally later on Santiago. While a few juveniles had left the nest, most nests had nestlings. Thus, more data on nesting success were available. The occurrence of pairs of fledged young and the great abundance of food remaining in the nests suggest that most of these nestlings should have survived. Considering just the number of young of any size in a nest or recently fledged, monogamous pairs on Santiago produced 1 young at a time rather than the 2 or 3 of some of the larger groups (Table 3). If we look at reproductive success *per male,* however, monogamous males were producing more young, on the average, than males in multiple-male groups (1.0 vs. 0.6, respectively). Of 6 nests of polyandrous groups included here, only 2 (with 2 males each) were producing young at a better rate per male than monogamous males. Nesting records gathered by de Vries from 1969–1975 on Santa Fe suggest a similar pattern, with little difference in nesting success between polyandrous groups and pairs but greater per male success for monogamous males (Table 3).

*Survivorship of territorial and nonterritorial birds.*—A preliminary analysis of the returns of the 75 birds banded on Santiago in 1977 shows striking differences between the survivorship of territorial and nonterritorial birds. Five groups on territories were banded in 1977, and four of these were closely observed in 1979. Of 14 banded birds in the sample, 12 were still alive and in the same territory. Assuming unobserved birds had died (rather than having changed territories), survivorship was nearly 85% over 2 yr.

Of 56 nonterritorial birds banded in 1977, 11 were observed among birds at the goat carcass in 1979. Undoubtedly, some females entered the breeding population during this period, but extrapolating an 85% survivorship to the estimated 50 territories on Santiago would result in just seven vacancies. If we use the liberal figure

of 10 females entering the breeding population, we get only about 40% survivorship over the 2-yr period. Based on a somewhat smaller sample, the 1977 recapture rate of birds banded by de Vries in 1974 yielded a survival rate similar to the 1977–79 rate (50 birds banded, 12 birds recaptured, for 24% survivorship over 3 yr). While these two estimates of survivorship are rather crude, we are convinced of the presence of different survival rates between territorial and nonterritorial birds.

## DISCUSSION

*The adaptive significance and evolution of cooperative polyandry.*—Previous studies of cooperative breeding have explained the evolution of adult helpers by showing both increased production of young, which makes helping beneficial to the parents, and increased long-term fitness for the helper, who may eventually find or inherit a territory and have helpers of his own (see Brown 1978 for a review). Cooperative systems have often evolved in habitats that are stable and saturated in such a way that a young bird cannot immediately find a location in which to breed (Selander 1964, Gaston 1978). Staying in the safety of a territory and working for a better breeding position is more productive than searching for a nonexistent territory. Cooperative breeding can also evolve in nonstable habitats, however (Brown 1978). If fluctuations in climate and/or resources result in fluctuating juvenile mortality, then "bet-hedging" life-history traits might evolve (Stearns 1976). These traits (late maturity, long life, small clutches, etc.), again combined with low dispersal ability, could also result in communal living. In fact, conditions that differentially favor selection for adult survivorship could result in cooperative breeding with adult, breeding helpers.

Harris' Hawks in the arid deserts of southern Arizona face erratic rainfall patterns (from 0.43 cm to 14.3 cm) and utilize food resources that are spatially and temporally unpredictable (Mader 1975a, b; 1979). Although little is known about group formation or relatedness, the Arizona populations are cooperatively polyandrous. In contrast, Harris' Hawk populations in west Texas are highly nomadic, and polyandry is rare (Griffin 1976). [Brown (1978) suggests nomadism as an alternative result of unpredictable rainfall patterns if dispersal ability is good. Why there is a difference in dispersal ability between two hawks in west Texas and Arizona is not clear.]

In the Tasmanian Native Hen, flightlessness results in low dispersal of young and creates highly concentrated areas of adults. This habitat saturation and maintenance of family groups results in sets of brothers sharing a female (Ridpath 1972). Although Ridpath describes the semi-arid climate of the Tasmanian Midlands as stable, he does so in comparison to the climate faced by the Australian Black-tailed Native Hen (*Tribonyx ventralis*), again a highly nomadic species. Rainfall during his study varied from 28 to 86 cm, and reproduction doubled in good years. This variation in rainfall is probably not as unpredictable as that found in Arizona, but the Tasmanian Native Hen has 2-yr-old nonbreeding helpers in addition to adult trios.

Drawing from the observations above, we can speculate about the adaptiveness and evolution of polyandry in the Galapagos Hawk. The hawk is a long-lived bird existing in an isolated and saturated habitat, so some form of cooperative behavior is not surprising. Kinship of breeding males seems unlikely (see below). Juvenile helpers are absent, but this also is not surprising, as young helpers in as specialized a forager as a hawk may be inefficient and therefore ineffective compared to the

standard small passerine. It is interesting to note that for many cooperative breeders, including the Tasmanian Native Hen (Ridpath 1972) and the Florida Scrub Jay (*Aphelocoma coerulescens*) (Woolfenden 1975), the increased reproductive output of cooperative groups was most evident in post-fledging survivorship. In the hawk, young are expelled from the territory a few months after fledging no matter how many parents there are. The presence of unrelated extra adults rather than juveniles on territories would make it more difficult to establish a dominance hierarchy that would exclude breeding by some birds.

For polyandry to be adaptive in the Galapagos Hawk, a male willing to join a cooperative group must produce, on the average, more offspring in his lifetime than a bird practicing only monogamy. Our data showed that polyandrous groups were producing more young per territory than monogamous pairs. Polyandrous males, however, produced fewer offspring per breeding attempt than monogamous males. Even if there is differential fertilization by males, polyandry represents a loss of confidence of paternity, a considerable disadvantage in a species with high paternal investment. For this system to evolve, there must be advantages that outweigh this loss in short-term reproductive success.

One obvious advantage would be an increase in survivorship for polyandrous birds. If a male in a group produces fewer offspring per year (on the average) but survives to breed for a longer period than the average monogamous male, the cooperative male may be more fit. Although there is not sufficient data to test this yet for the Galapagos Hawk, in the Harris' Hawk polyandrous males do survive better than monogamous males (Mader 1979). Certainly, the present-day choice for the Galapagos Hawk of entering a territory with low per-male reproduction but high survivorship may be more adaptive than staying in the highlands with higher mortality during the long search for a monogamous territory. Most studies of cooperatively breeding adults show better survivorship of adults, rather than offspring, as the result of cooperation (Vehrencamp 1977, Fry 1972, Dow 1978, Mader 1979).

The possibility also exists that the final reproductive reward is achieved by the male who out-survives his cooperators and gets a few years of monogamous breeding in addition to several cooperative years. If being part of a cooperative group is a better pathway to monogamy than waiting, cooperators should dominate the system. Male Noisy Miners, for example, cooperate to improve colony quality, increase survivorship, and live to become the dominant breeder (Dow 1978).

*Kinship and polyandry in the Galapagos hawk.*—One other possible advantage of cooperative polyandry is increased reproductive success through inclusive fitness. Kinship has been considered an important aspect of the evolution of cooperative breeding (Brown 1978). Birds helping to raise young of closely related birds are in fact aiding themselves through inclusive fitness (Hamilton 1964). While the role of inclusive fitness may be important in some species and certainly not disadvantageous in others, several recent studies have shown that helping may result in increased lifetime fitness for an individual even when unrelated offspring are helped (Woolfenden and Fitzpatrick 1978, Brown 1978, Emlen 1978, Ligon and Ligon 1978). In polyandrous mating systems, cooperating sets of brothers would achieve greater genetic rewards than sets of randomly related males. In the Tasmanian Native Hen, sets of brothers share a female (Ridpath 1972). Trios of native hens defend a larger territory and produce more young than do monogamous pairs, and males, when brothers, have a high genetic relatedness to all the young. The loss of confidence in

paternity in polyandry is thus outweighed by gains in total reproductive success and by inclusive fitness (Maynard Smith and Ridpath 1972, Emlen 1978).

Given the proposed dynamics of group formation (see below) and the breeding biology of the Galapagos Hawk, however, there seems little chance that groups of brothers are forming. Although in very lush years two young per nest are occasionally produced, one offspring per year is the most frequent fledging rate. This young is chased from the territory a few months after fledging. In about 3 yr it achieves adult plumage and is ready to join a breeding group. Breeding groups comprising three and four males occur regularly on Santiago. If we assume one young per year with every other young a male, it would take an average of 7 yr to produce four male siblings plus 3 more yr for the youngest bird to become an adult. This would be a long period for the oldest brothers to wait before breeding, and the rareness of adult males in the highlands of Santiago suggests strongly that they do not. Although isolation of the islands, coupled with low dispersal between islands, would create some degree of inbreeding, kinship probably is not an important factor in the maintenance of this breeding system.

*Polyandry as the mating system.*—We do not yet have a good explanation for why the Galapagos Hawk has a polyandrous system rather than some other cooperative system. One obvious possibility is that polyandry is the result of a skewed sex ratio. Evidence from other cooperatively polyandrous species has shown either a skewed primary sex ratio (Maynard Smith and Ridpath 1972) or differential adult mortality favoring males (Mader 1979, Ridpath 1972). Because of the presence of unmated females, this seems less true for the Galapagos Hawk. Although there is a bias toward males on the islands, there is apparently no shortage of available mates. Furthermore, the highest frequencies of polyandry and the largest groups are found on the island with the most unmated females. This is contrary to what one would expect if a skewed sex ratio were driving the system toward polyandry.

A second possibility is that in these birds females are the more competitive sex. Theoretically, intersexual differences in reproductive investment should result in more male than female helpers (Whitney 1976), and this is, in fact, the case (Brown 1978). There is apparently considerable aggression among females in most cooperative species (for examples, see Vehrencamp 1977, Emlen 1978, Dow 1978). This might be especially true for hawks, where females are the larger, more aggressive sex and tend to control activities around the nest.

*The formation and dynamics of polyandrous groups.*—When a territory opens because of the mortality of breeding birds, several males may move into the area and mate with either the old female or a new female. Although very few cases of group formation have been observed (de Vries 1973), there appears to be a critical period of group bonding. After this period, intruding males and females are quickly chased away. Our data suggest that once a bird establishes itself on a territory, it remains there for life. Group size does not appear to be highly flexible from year to year; as mortality occurs, group size generally gets smaller. If groups are this rigidly structured, at least some of the monogamous pairs observed may be remnants of larger groups. Given the above system, the number of polyandrous groups on an island should be a reflection of the pool of birds available when a territory opens. If many adult males are available, many large groups might be expected to form. If few males are available, however, smaller groups or monogamous pairs may result. Again, this hypothesis does not depend upon a skewed sex ratio. Even if

mortality rates for territorial birds in these two situations were similar, then monogamous territories would become open more often, and smaller (2-male) polyandrous groups would become monogamous more rapidly. Thus, islands with relatively small pools of available males would more rapidly deplete the pool of males that does exist. Santa Fe has fewer excess males than Santiago, more monogamous pairs, and smaller polyandrous groups. Because of its extensive habitat for nonterritorial hawks, Santiago is able to maintain a large pool of birds ready to move into territories and thus has larger groups more frequently. In general, we should expect that yearly fluctuations in survival and reproductive rates could affect this pool of excess birds and thus affect the size and frequency of polyandrous groups on an island.

Thus, cooperative polyandry in the Galapagos Hawk shares many traits with other cooperative systems. In this case, long-lived birds in a saturated environment may be attempting to maximize reproduction by increasing the length of their reproductive period through group breeding, despite the reduction in average yearly investment. While the lack of suitable territories in the Galapagos Islands may be among the ultimate causes of the evolution of this system, variation in resources and hawk survivorship from island to island [the "richness" mentioned by de Vries (1973)] seem to serve as proximate factors causing the variation in the frequency of polyandrous groups on these islands.

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